

NEWS AND VIEWS

PERSPECTIVE

Recurrent adaptation in a low-dispersal trait

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The study of natural populations from contrasting environments has greatly enhanced our understanding of ecological-dependent selection, adaptation and speciation. Cases of parallel evolution in particular have facilitated the study of the molecular and genetic basis of adaptive variation. This includes the type and number of genes underlying adaptive traits, as well as the extent to which these genes are exchanged among populations and contribute repeatedly to parallel evolution. Yet, surprisingly few studies provide a comprehensive view on the evolutionary history of adaptive traits from mutation to widespread adaptation. When did key mutations arise, how did they increase in frequency, and how did they spread? In this issue of *Molecular Ecology*, Van Belleggem *et al.* (2015) reconstruct the evolutionary history of a gene associated with wing size in the salt marsh beetle *Pogonus chalceus*. Screening the entire distribution range of this species, they found a single origin for the allele associated with the short-winged ecotype. This allele seemingly evolved in an isolated population and rapidly introgressed into other populations. These findings suggest that the adaptive genetic variation found in sympatric short- and long-winged populations has an allopatric origin, confirming that allopatric phases may be important at early stages of speciation.

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Wet feet

The ground beetle *Pogonus chalceus* occurs in salt marshes along the coasts of Atlantic and Mediterranean Europe

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(Fig. 1). Wing size in this species varies from short to fully developed. This variation is seemingly influencing how often and how long these beetles are willing to stand wet 'feet' in habitats that regularly inundate. Populations with strongly reduced wing size are found in tidal marshes where inundations are predictably short, that is maximally six hours. Accordingly, when the tide comes in, short-winged beetles trap an air bubble and submerge, waiting for better times. In contrast, long-winged populations are found in seasonal marshes where the duration of inundation is unpredictable (Fig. 1). Accordingly, upon inundation, long-winged beetles take off and look for drier places. Indeed, the retention of long wings, which is thought to be energetically costly, is argued to be an adaptation as a consequence of which beetles can escape long-term inundations (Desender *et al.* 1998).

Along the Atlantic coast, both short- and long-winged populations can be found, sometimes in very close proximity (i.e. 10–20 m; Fig. 1). In one of the first genetic studies on these populations, it was discovered that allelic variation at an allozyme locus, the mitochondrial isocitrate dehydrogenase (*mtIdh*) gene, strongly correlates with mean population wing size and deviates markedly from neutral expectations (Dhuyvetter *et al.* 2004). By comparing gene flow between pairs of sympatric short- and long-winged populations, it was concluded that ecology-dependent reproductive isolation might be driving parallel speciation in *P. chalceus* (Dhuyvetter *et al.* 2007).

Salt marsh beetles hence provide an interesting model system for replicated adaptation and ecological speciation. As such, they deserve a place among other taxa that are illustrative for parallel evolution, such as the three-spined stickleback and stick insects. One complication in the work on *P. chalceus* is that wing size is polygenic and that the functional link with *mtIdh* is unclear. However, Van Belleggem *et al.* (2015) show that *P. chalceus* stands out for another reason: the system is old enough to observe parallel evolution of an adaptive phenotype, yet young enough to trace back the original mutation. A comprehensive view on both the origin and spread of a gene associated with adaptation and ecological speciation has been rarely achieved in any other model.

A selective sweep of a low-dispersal trait

Using samples throughout almost the entire distribution range, Van Belleggem *et al.* (2015) first reconstructed a *mtIdh* gene tree for *P. chalceus* (Fig. 1). They then performed coalescent simulations and approximate Bayesian computation to compare alternative scenarios for the evolution of both ecotypes. They show that the *mtIdh*-B allele, associated with long-winged populations, is ancestral and

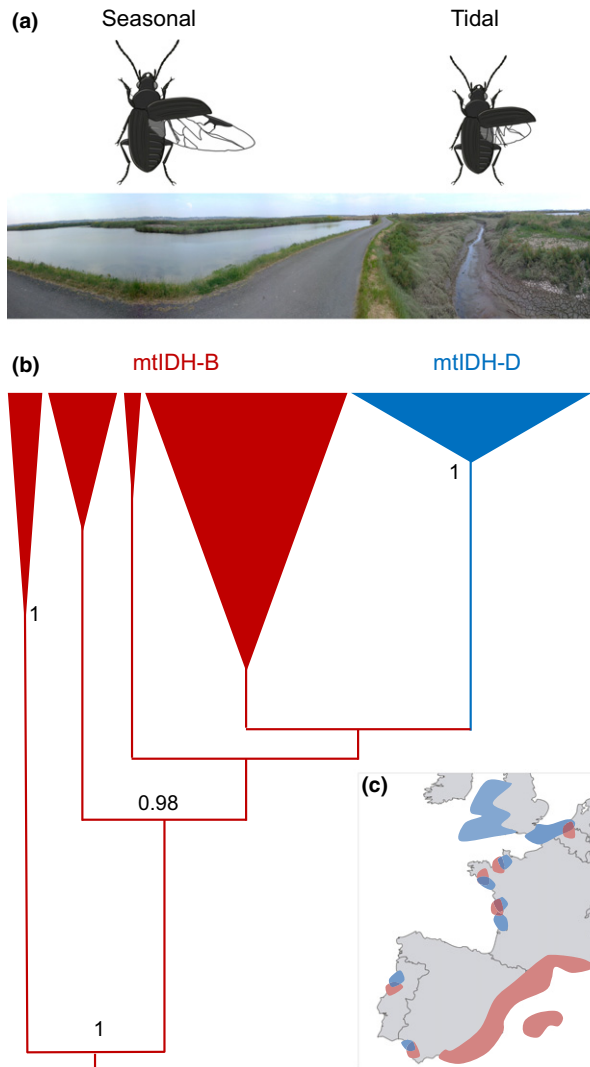


Fig. 1 (a) The ancestral long-winged and derived short-winged ecotype of *Pogonius chalceus* in their respective habitat. While the long-winged ecotype occupies inland water bodies, the short-winged ecotype occupies tidal marshes near the shore. As shown on the picture, both habitat types are sometimes in very close proximity. (b) Bayesian *mtldh* gene tree covering nearly the entire species range, with lineages associated to the long-winged and short-winged ecotype in red and blue, respectively. Numbers indicate posterior probabilities. Rapid and repeated introgression of the *mtldh*-D allele associated with the short-winged phenotype most likely explains the widespread occurrence of short-winged populations and the repeated adaptation to tidal habitats. (c) Distribution of sampled long-winged (in red) and short-winged (in blue) populations in Europe.

that the *mtldh*-D allele, associated with short-winged populations, evolved only once. This divergence occurred between 0.047 and 0.165 Ma. From the coalescent simulations, the authors conclude that the derived allele probably evolved in a partially isolated population, as suggested by the deep divergence and a strongly reduced recombination

rate between the *mtldh*-B and *mtldh*-D sequences. Subsequently, the *mtldh*-D allele spread along the Atlantic coast in a selective sweep-like fashion resulting in reduced divergence among the *mtldh*-D sequences (Fig. 1). As the *mtldh*-D allele associated with the short-winged ecotype is dispersal-limited, it is unclear how this has happened. Potential colonization mechanisms of the low-dispersal trait include spread by long-winged individuals, analogous to the mechanism of 'allelic recycling' hypothesized for the *Eda* gene in stickleback (Bell & Aguirre 2013; Raeymaekers *et al.* 2014), or transport of eggs by birds or flood debris.

Wing size in salt marsh beetles has a high heritability ($h^2 = 0.80\text{--}0.90$), making it an easy target for selection (Desender 1989; Van Belleghem & Hendrickx 2014). Interestingly, the tight association of the *mtldh* alleles with the different dispersal strategies upon flooding in *P. chalceus* might directly contribute to reproductive isolation. More precisely, long-winged individuals may avoid, or suffer from, the daily inundations in the tidal areas inhabited by short-winged individuals. This may create barriers to gene flow, in particular for genes underlying dispersal-linked traits. Dispersal-linked loci play a crucial role in the responses of metapopulations to landscape dynamics (Hanski *et al.* 2004), but are not necessarily involved in local adaptation (e.g. Hendrickx *et al.* 2013). In *P. chalceus*, metapopulation dynamics and local adaptation might be inevitably intertwined by targeting the same genes. This possibility may be extrapolated to a mechanism for the evolution of short-winged species, which has occurred repeatedly in beetle diversification (den Boer 1970).

The elegant features of the *P. chalceus* model give wings to further research. The availability of a transcriptome (Van Belleghem *et al.* 2012) and draft genome (in preparation) opens opportunities to map the genomic basis of wing size and to evaluate the consequences of reduced gene flow at the genome-wide level. In addition, experimental tests of mating preferences and habitat choice are underway to identify the behavioural drivers of reproductive isolation in *P. chalceus*. Among approximately 400 000 beetle species (40% of all insect species), few are famous models for speciation research. Salt marsh beetles might soon become an exception to this rule.

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